OBSERVATIONS ON DEVELOPMENT OF THE HETEROPOD MOLLUSCS *PTEROTRACHEA HIPPOCAMPUS* AND *FIROLOIDA DESMARESTI*[1]

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ABSTRACT

The nidamentary filaments and various developmental stages up to veliger larva of *Pterotrachea hippocampus* Philippi 1836 and *Firoloida desmaresti* Lesueur 1817 are described and illustrated. General information on the late veliger and the newly metamorphosed female of the latter species is included. Apparently the filament of *P. hippocampus* is a typical "egg string" which serves to encase only one batch of spawn whereas that of *F. desmaresti* is a permanent structure. In the laboratory, both species developed from fertilized egg to free-swimming larva in approximately 48 hours.

INTRODUCTION

Because of the curious adaptations of heteropods to their holoplanktonic existence, their reproduction and development are of special interest. Some observations on *Pterotrachea hippocampus* Philippi 1836 (Fig. 1A) and *Firoloida desmaresti* Lesueur 1817 (Fig. 1B), among the most highly modified species of the group, can be added to the scant information on development of Heteropoda summarized by Raven (1958). These concern the nidamentary filament and embryos of both species and a single veliger of *Firoloida desmaresti* which metamorphosed overnight in the laboratory. All specimens were collected with DISCOVERY-type plankton nets from the upper 25 m of the Florida Current off Miami.

Tesch (1949) commented that probably all heteropods produce egg-strings in which the embryos develop to the veliger stage and that internal fertilization, perhaps via spermatophore, should occur, but that transfer of sperm has never been observed. In fact, the process of insemination in many holopelagic dioecious animals as well as monoecious ones such as chaetognaths remains a matter of conjecture. The spawning of *Firoloida desmaresti* was described by Lamy (1928), who reported that in winter and spring the female bears a nidamentary filament which may measure 0.4 mm in diameter and grow nearly as long as the body (30 mm). This remains attached, receiving embryos which pass from the uterus when segmentation is nearly complete and are gradually pushed by successive spawn to the open extremity where they emerge as free-swimming larvae. The present data indicate that in this species the nidamentary filament is not a seasonal production but a permanent part of the female anatomy.

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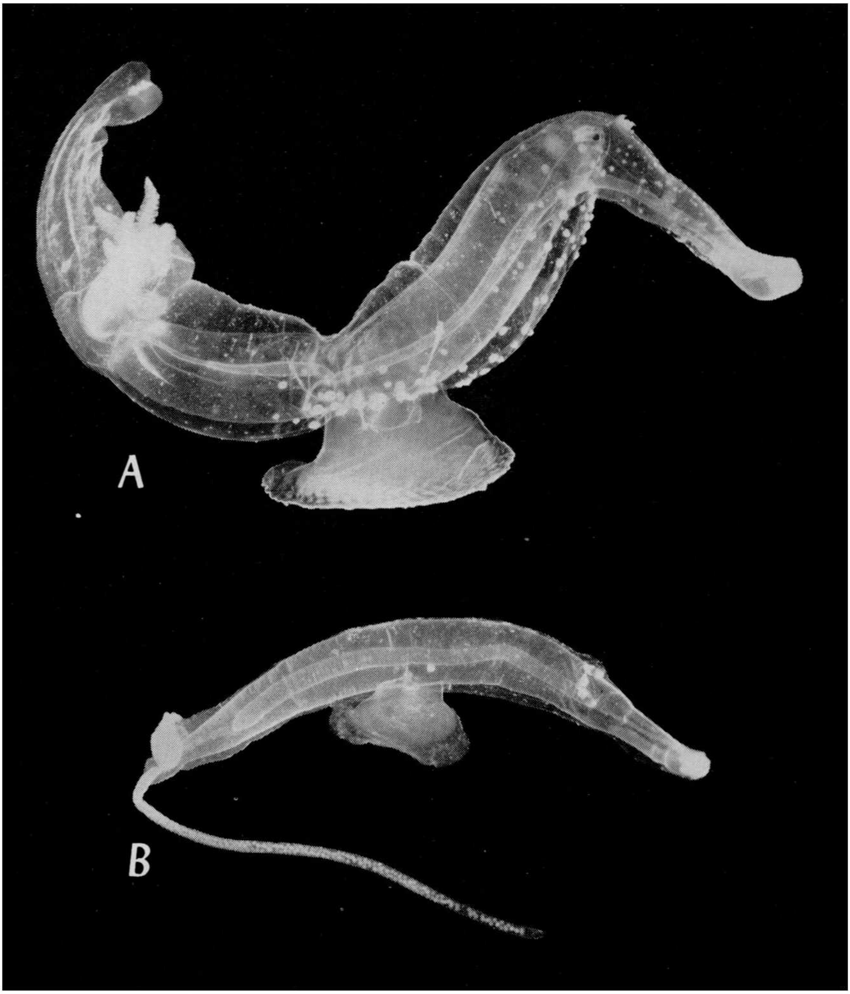

FIGURE 1. A, *Pterotrachea hippocampus*, adult ♀, ×3.2. — B, *Firoloida desmaresti* adult ♀, ×4.

OBSERVATIONS

Pterotrachea hippocampus.—One female was caught at a depth of 10 m in the forenoon of May 7, 1963. The adult size range is 20-80 mm (Tesch, 1949); this specimen was 46 mm long. Probably in response to an abrupt change in environment, particularly a higher temperature, it produced an egg-string approximately 250 mm long between 1400 and 1600 hours of that afternoon. In the cylindrical gelatinous filament, 0.31-0.34 mm in diameter with a wall 0.05 mm thick (Fig. 2), encapsulated uncleaved eggs were regularly spaced about 0.12 mm apart. Since, in *F. desmaresti,* segmented embryos are extruded into the filament, it seemed that this was an abnormal spawning induced by laboratory conditions. However, within 14 hours all embryos in the filament had begun development. Those closest to the parent were two-celled, with inequal blastomeres AB and CD, and the remainder were blastulae. Six hours later, these embryos were, respectively, ovate blastulae of very small micromeres and large, yolky macromeres, and gastrulae. The blastocoel could not be seen; it is either very small or nonexistent. Epiboly and invagination produced gastrulation.

On the morning of the following day, May 9, 16 hours after the previous observation, the younger embryos were in late trochophore stage and the older ones were early veligers. All were rotating. No apical cilia were seen; the prototroch, located close to the animal pole, appeared incomplete. Six hours later, the capsules of the older veligers began to break down and the emergence of veliger larvae (Fig. 2) from the filament commenced. These were shell-less, with a thin but distinct operculum, ciliated velar ridge, foot primordium and visceral hump containing, ventrally, two large anal cells. A prominent telotroch was present in contradiction to the statement in Raven's (1958) compilation that there is no telotroch in the Heteropoda, ". . . only two protruding anal cells . . ., which may bear some fine cilia, but no ciliary tuft."

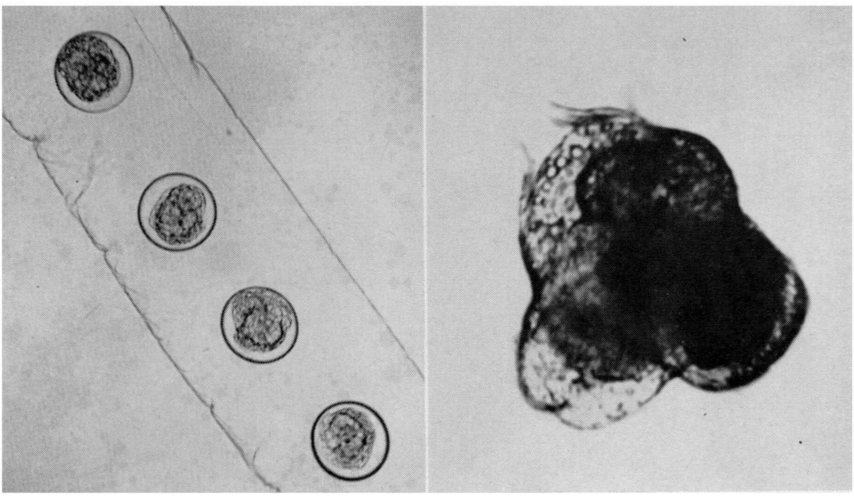

FIGURE 2. *Pterotrachea hippocampus:* left, portion of the nidamentary filament containing embryos in early veliger stage, ×81; right, free swimming veliger, ×214.

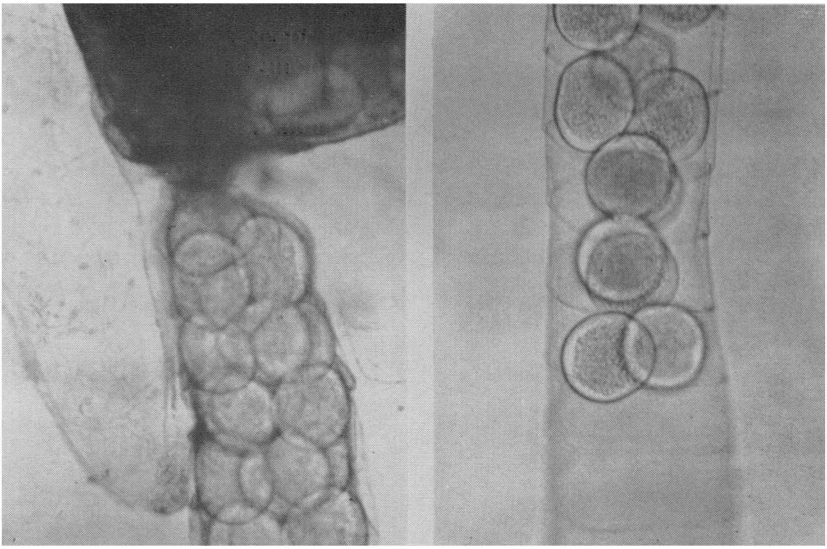

FIGURE 3. *Firoloida desmaresti:* left, proximal portion of nidamentary filament, ×74; right, distal portion of nidamentary filament, ×74.

For several reasons, primarily the lack of adequate facilities at that time, no attempt to rear the larvae was made. However, the adult with embryos was kept in Florida Current water in an air-conditioned room. It can be assumed that production by a female ready to spawn of the nidamentary filament with fertilized eggs and development of the embryos was nearly, if not completely normal.

Firoloida desmaresti.—Numerous females with nidamentary filaments were caught at 25-20 m between 1000 and 1100 hours on May 15, 1963. The filaments of specimens measuring 17-30 mm were 22-32 mm long. The uterus was enlarged by cleaving embryos, and those which had just emerged into the filament were in, approximately, the 32-cell stage. These were not regularly spaced as in *P. hippocampus* but packed closely and at random within the annulated filament (Fig. 3). Toward the distal extremity, veligers which had just emerged from their capsules tended to space themselves so that the annulations of the filament could be seen clearly (Fig. 3).

In Figures 4-6, several stages of the developmental sequence are shown, beginning with a 32-cell stage, which had just entered the filament (Fig. 4A). The proximal half of the filament contained blastulae, all stages of gastrulating embryos and trochophores, and the distal half, late trochophores, early veligers and, finally, veligers which had just emerged from the capsule and were ready to hatch. Raven (1958) noted the marked flattening of the vegetative side of the blastula just before gastrulation, resulting in a placula form which gastrulates by an incurving followed by epiboly in "Firoloides" *(Firoloida)* (Figs. 4B,C) and *Carinaria*. After gastrulation (Fig. 4D), a gradual development of reddish-purple pigment in the large entoderm cells eventually results in a purple gut. Presumably this is the origin of the pinkish purple pigmentation of the adult visceral mass. The trochophore (Fig. 5A) lacks teletroch and apical tuft, although the apical plate is ciliated; the prototroch is well developed and the two anal cells are prominent. After differentiation of the velar ridge from the prototroch and of the foot primordium have begun (Fig. 5B), a yellow-brown mass of cells becomes apparent on the posterior dorsal surface of the visceral hump (Fig. 5C). This is the shell gland, which then sinks below

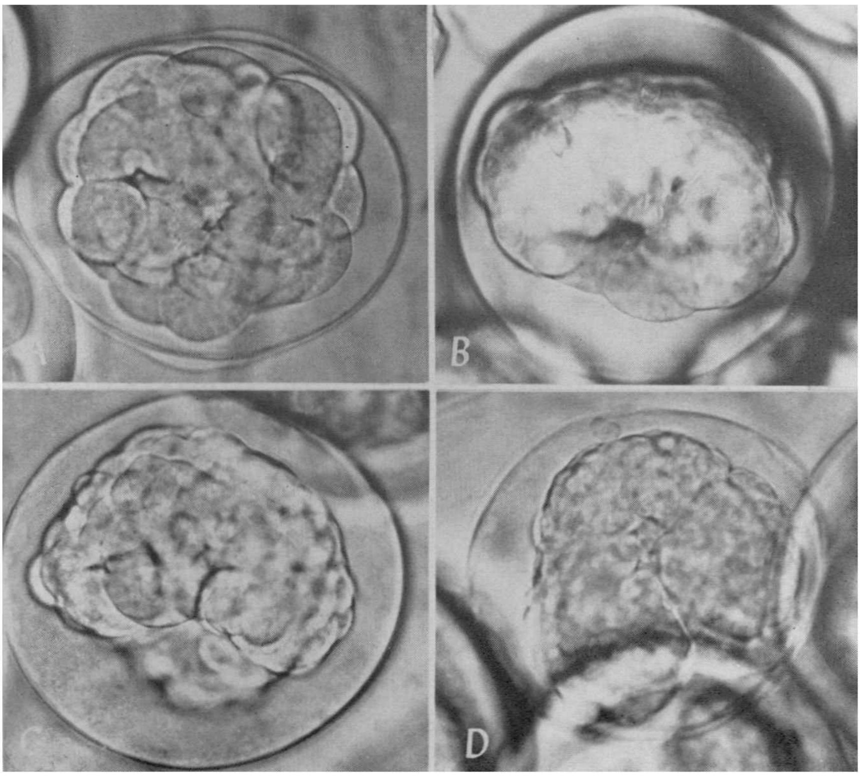

FIGURE 4. *Firoloida desmaresti:* A, 32-cell stage, ×140; B, gastrula, showing blastopore, ×141; C, gastrula, lateral view, ×150; D, gastrula in optical longitudinal section, showing archenteron, ×134.

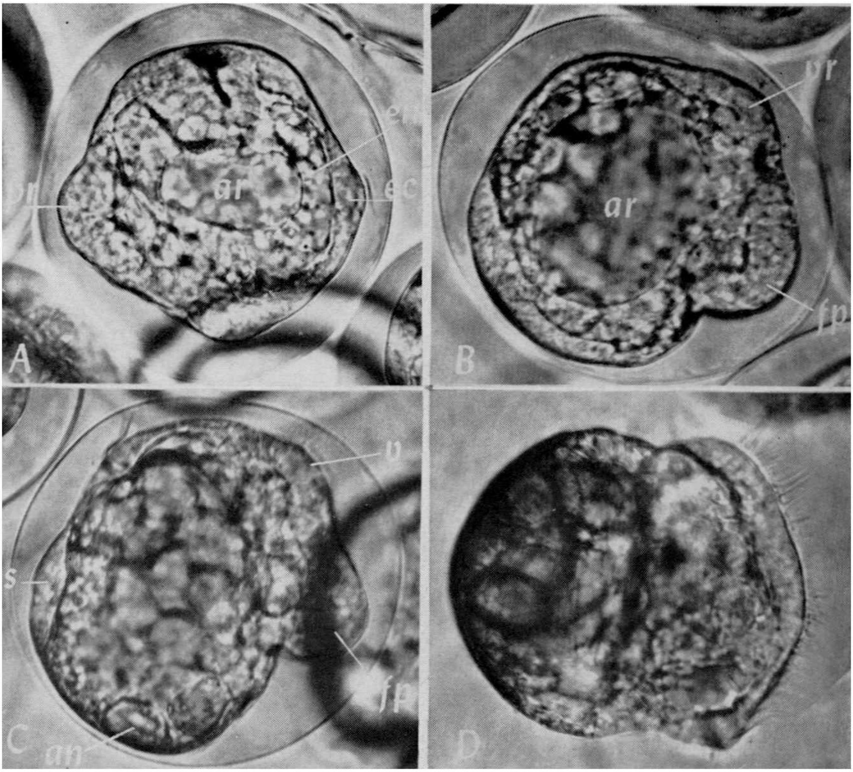

FIGURE 5. *Firoloida desmaresti:* A, trochophore in optical longitudinal section, ×135; B, early veliger stage, ×132; C, early veliger stage, ×134; D, veliger larva, dorsal view, ×143. (Lettering: *an*, anal cell; *ar*, archenteron; *ec*, ectoderm; *en*, entoderm; *fp*, foot primordium; *s*, shell gland; *v*, velum; *vr*, velar ridge.)

the epidermis, forming a large, discrete structure. No evagination was observed. Had one of the larvae not cast its shell while still in the filament, it would have been nearly impossible to observe this extremely fragile, cuticular protoconch. It was colorless and cap-shaped, with a ragged edge. The major development of the veliger takes place after hatching. The visceral hump of the newly emerged larva is encased in its frail shell, the ciliated foot bears a tiny operculum and the velum is an unlobed ridge (Figs. 5D, 6).

Although no further observations of these larvae were made, there are data on the late veliger and the young adult of *F. desmaresti* just after metamorphosis (Owre, 1949). On March 13, 1948, one advanced veliger was isolated from plankton collected at approximately 20 m. It had a

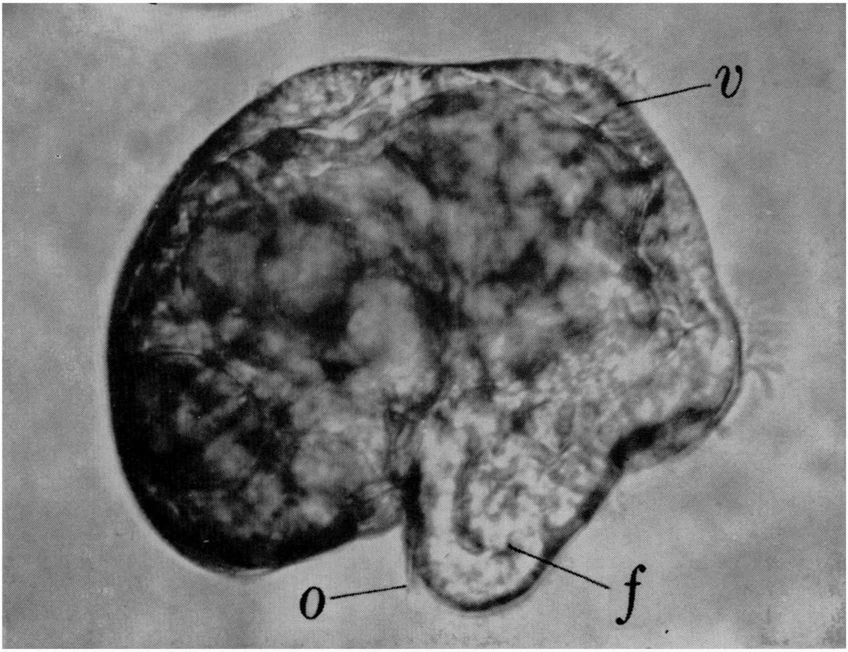

FIGURE 6. *Firoloida desmaresti:* veliger larva, ×243. (Lettering: *f*, foot; *o*, operculum; *v*, velum.)

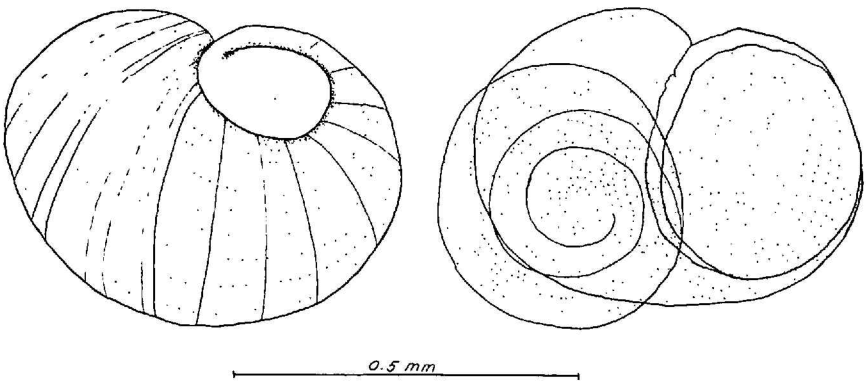

FIGURE 7. *Firoloida desmaresti:* larval shell cast off at metamorphosis; left, apical view; right, apertural view showing discarded operculum.

velum of four elongate lobes and a dextral shell (Fig. 7) of two whorls. The two right lobes of the velum measured from tip to tip 0.8 mm and the diameter of the shell was 0.4 mm. The shell was covered with minute depressions and bore faint vertical striations or growth lines. The large, round aperture, 0.31 mm in diameter, was surrounded by a conspicuous lip. The horny, concave operculum was dextrally concentric. The larva was colorless and transparent, and the shell, horn-colored.

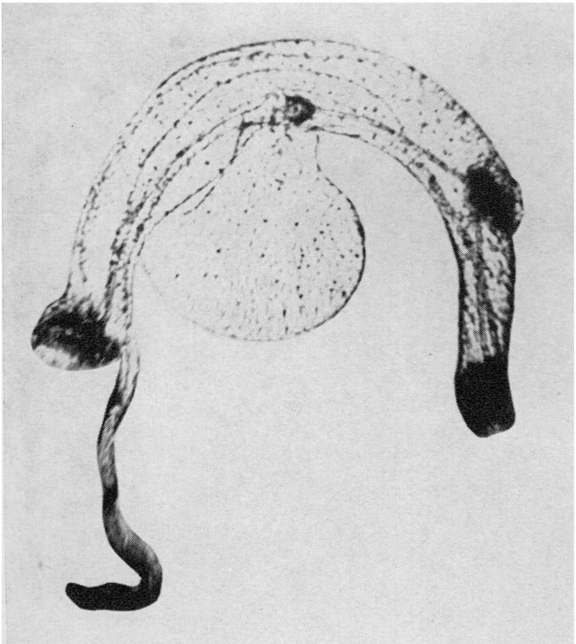

FIGURE 8. *Firoloida desmaresti*, newly metamorphosed, ×97.

When last observed in the early evening, the larva was swimming actively in its dish. Fifteen hours later, the dish contained an empty shell with the operculum pushed to one side of the aperture and a minute *F. desmaresti* (Fig. 8). Although the body was only 1.2 mm long, it showed all the gross morphological characteristics of the adult, including a nidamentary filament approximately 0.5 mm in length. The proboscis, eyes, swimming fin and visceral sac (nucleus) were well developed. Nerves and ganglia, esophagus and intestine could easily be traced in the transparent body. Tentacles, characteristic of the male, were absent, but a rudimentary fin-sucker, thought to occur only in males, seemed to be present. It was very small and difficult to see in the living animal. In the photograph (Fig. 8), it appears as a dark patch on the anterior edge of the swimming fin. In view of the lack of facilities for rearing larvae at that time, it was a mistake not to have preserved the animal for it died and disintegrated during the night of March 14, about 24 hours after metamorphosis.

Discussion

Both species develop from fertilized egg to free-swimming veliger in approximately 48 hours in the laboratory. When *P. hippocampus* spawns, it gradually extrudes a long filament containing encapsulated fertilized eggs, regularly spaced within a transparent gelatinous matrix. The filament is an egg-case basically like the protective covering in which most gastropods deposit their embryos. Probably it is a temporary structure, serving for the encasement of one batch of spawn only. In *Firoloida*, however, the nidamentary filament seems to be a permanent structure, present even in the tiny newly metamorphosed female. Its length varies from somewhat less than half that of the immature female to approximately the same as the mature specimen up to 30 mm (Florida Current material; Lamy, 1928). Tesch (1949) did not mention the length in his specimens, the largest of which were 40 mm long. In contrast, the egg-string of *P. hippocampus* was over five times the length of the female. The annulations of the shorter filament of *F. desmaresti* presumably make it a more durable structure than that of *P. hippocampus*.

The size at which these species become sexually mature is unknown. Tesch (1949) reported that females of *F. desmaresti* 10 to 40 mm long bore egg-strings but he did not state whether or not those of the smaller specimens contained embryos. There is no information on growth rate or frequency of egg-laying, which may well be virtually continuous. Certainly the "production line" method of reproduction in *F. desmaresti* is highly successful, for this species, cosmopolitan in tropical and subtropical waters, is extremely common. Tesch found it far more numerous than the Carinariidae and any of the other Pterotracheidae.

The development of shell in *P. hippocampus* should be studied. Although the adult is shell-less, as is *F. desmaresti*, it would be very unusual for the veliger to lack a shell. Probably a cuticular covering, undetected in the one group of veligers observed, develops before hatching, and the major growth of shell and velar lobes as well as morphological differentiation occur during larval life as they certainly do in *F. desmaresti*. As Tesch stated regarding *F. desmaresti*, "it is remarkable that no naturalist, so far, has been tempted to study the development of these eggs," and it is in order to stimulate study of development and, particularly, to record a spectacular metamorphosis that these observations are presented.

Sumario

Observaciones en el Desarrollo de los Moluscos Heterópodos *Pterotrachea hippocampus* y *Firoloida desmaresti*

Se describen e ilustran los filamentos nidamentarios y varios estados embrionarios hasta llegar a la larva veliger de *Pterotrachea hippocampus* Philippi 1836 y *Firoloida desmaresti* Lesueur 1817. Se incluye información general de la última veliger y la recién transformada hembra de la especie últimamente mencionada. Aparentemente el filamento de *P. hippocampus* es un típico "cordón de huevos" que sirve para alojar sólamente un desove, mientras que el de *F. desmaresti* es una estructura permanente. En el laboratorio, ambas especies se desarrollaron desde el huevo fertilizado hasta larvas libres, en 48 horas.

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